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Author(s): Veryl E. Becker
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Nitrogen Fixing Lichens in Forests of the Southern Appalachian Mountains of North Carolina[1]

VERYL E. BECKER[2,3]

Abstract. *The abundance and species diversity of nitrogen fixing lichens were determined for several forests of the southern Appalachian Mountains of western North Carolina. Gray beech forests of wet, high-elevation beech gaps were auspicious locations for these lichens. The bark of* Aesculus octandra *Marshal was the optimum habitat, particularly for the dominants* Lobaria quercizans *Michx. and* Lobaria pulmonaria *(L.) Hoffm. Lichen biomass in this gray beech forest commonly ranged from 7 to 9 kg ha^{-1} but was higher where* Aesculus octandra *was abundant. Lichens were less abundant in oak forests and cove forests, and none was found on conifers. The annual contribution of ammonia nitrogen by lichens was roughly estimated to be 0.8 kg ha^{-1} for the gray beech forest in beech gaps.*

The southern Appalachian Mountains are known for their scenic beauty, abundant rainfall and vegetation which is rich in community types and species diversity. Meteorological records taken along the southern limits of the Blue Ridge escarpment and the adjoining mountain ranges indicate that annual precipitation commonly approaches or exceeds 200 cm yr^{-1}. In the gorges along the Blue Ridge escarpment values exceeding 250 cm yr^{-1} occur with regularity (Cooper, 1963). Warm moist air from the south rises, as it moves from the flat Piedmont of Georgia and South Carolina, cools and loses this moisture as it proceeds into these mountainous areas.

The combination of high rainfall and great diversity in habitats found in these old and geologically stable mountains has led to considerable complexity in the types of climax forests found there (Whittaker, 1956). Representatives of the northern boreal forests are found at high elevations, cove hardwood forests are common in many of the mesophytic locations, a variety of oak forests occupy the majority of the landscape and several other forest types are interspersed within these communities.

From previous publications on the nitrogen fixing lichens it appears that there is an association between the abundance of these lichens and the moisture available to the lichen. In the arctic, where these lichens have been implicated as important contributors of reduced nitrogen (Kallio & Kallio, 1975; Schell & Alexander, 1973; Crittenden, 1975), moisture is not a limiting factor. In an investigation of the Colombian montane rain forest Forman (1975) estimated that the biomass of these lichens was 5.7 kg ha^{-1} and that the annual rates of nitrogen fixation were in the range of 1.5 to 8 kg N ha^{-1}. In the tall Douglas fir forest of Oregon Denison (1973) reported a nitrogen fixing lichen biomass of 390 to 500 kg ha^{-1}. Precipitation in the tropical rain forest is considered to be between 200 to 300 cm yr^{-1} (Forman, 1975) and in the tall Douglas fir forest is greater than 200 cm yr^{-1} (Zobel et al., 1976). These two forested areas, however, vary in the annual distribution of that

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[2] Department of Biology, Wake Forest University, Winston-Salem, NC 27109.
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TABLE 1. Determination of standard dry weight cm^{-2} values for nitrogen fixing lichens. Entries are mean ± one standard deviation of the weight in mg cm^{-2} with the number or replicates in parentheses.

Lichen	Dry Weight, mg cm^{-2}
Coccocarpia cronia (Tuck.) Vain.	12.8 ± 4.0 (10)
Collema subflaccidum Degel. [*Collema conglomeratum* Hoffm.]	10.3 ± 3.9 (10)
Leptogium corticola (Tayl.) Tuck.	13.9 ± 4.2 (13)
L. cyanescens (Ach.) Korb. [*L. chloromelum* (Ach.) Nyl.]	8.0 ± 2.5 (10)
Lobaria pulmonaria (L.) Hoffm.	17.3 ± 4.1 (18)
L. quercizans Michx.	19.8 ± 5.0 (19)
Nephroma helveticum Ach. [*Nephroma parile* (Ach.) Ach.]	11.4 ± 4.7 (10)
Pannaria rubiginosa (Ach.) Del.	19.9 ± 6.7 (10)
Parmeliella corallinoides (Hoffm.) Zahlbr.	33.1 ± 12.8 (10)
Peltigera canina (L.) Willd.	12.2 ± 2.4 (10)
P. polydactyla (Neck.) Hoffm. [*P. horizontalis* (Huds.) Boumg.]	12.5 ± 3.9 (11)
Pseudocyphellaria crocata (L.) Vain. [*P. aurata* (Ach.) Vain.]	19.1 ± 4.2 (10)
Sticta weigelii (Ach.) Vain. [*S. fuliginosa* (Dicks.) Ach.]	19.5 ± 3.7 (17)

precipitation. A uniform distribution of rainfall occurs in tropical rain forests, whereas in the tall Douglas fir forest most of the precipitation occurs during the winter months with the summers being exceedingly dry. By comparison the precipitation in the southern Appalachian Mountains of this study does not undergo appreciable seasonal variation.

The objective of the present study was to determine whether nitrogen fixing lichens were abundant in the southern Appalachian Mountains and to determine which of these lichen species were particularly prevalent. The premise of the investigation was that the abundance of annual precipitation and the diversity of vegetational communities within these mountains should result in a high nitrogen fixing lichen biomass and a large annual contribution of ammonia nitrogen to one or more of these forests.

MATERIALS AND METHODS

Field measurements were conducted during the summers of 1976, 1977 and 1978. Lichens were identified with the keys of Dey (1975, 1978) and Hale (1969) and by comparing specimens to those found in the Duke University Herbarium. The forest vegetational types were according to Whittaker (1956).

Lichen abundance was assessed in the field by analyzing the distribution of vegetation with 20 × 20 m quadrats. Preliminary studies indicated that this size quadrat was suitable in terms of the time required to complete the measurements and the amount of information obtained on the lichens in the forest stand in question. In each quadrat all trees and shrubs over 2.5 cm dbh were measured and identified. The nitrogen fixing lichen species on each tree and shrub were noted, and the surface area of each lichen was measured with a grid, as previously described (Becker et al., 1977). In some instances, where the lichens were found high on the trunk of the tree, measurements were made either with the aid of a ladder or the grid was extended up the tree with a cane pole. In the one instance at Buckeye Gap where the lichen biomass was very high (see Results) it was necessary to measure 6 of the 19 buckeye trees within the quadrat. Dry wt cm^{-2} for each species of lichen was estimated for a minimum of 10 samples of approximately 10 cm^2 (Becker et al., 1977), and the total lichen biomass for each tree and quadrat was then estimated.

After consultation with foresters and scientific investigators familiar with forest communities of western North Carolina, a survey of some of the suggested representative forest tracts was conducted during the first two summers of this study. Upon entering a forest tract a quadrat which typically represented the forest community was selected and the measurements were completed. A total of 30 such quadrats was measured in 8 forest types (see Table 2). The data from these survey quadrats was used to select two sites for more detailed studies. Oak forests and gray beech forests were found to be favored locations for these lichens (see Table 2), hence in selecting the sites for the detailed

TABLE 2. Abundance of nitrogen fixing lichens in forest communities of the mountains of western North Carolina. Data are the mean and one standard error (where possible to calculate) for 20 × 20 m^2 quadrats within each vegetational type.

Vegetational Type	No. of Quadrats	Lichen Abundance in 400 m^2	
		Surface Area, cm^2	Dry Weight, g
Cove Hardwoods	9	904 ± 321	13.1 ± 4.7
Gray Beech	5	33,094 ± 21,907	586 ± 370.7
Red Oak-Chestnut	5	4880 ± 1280	87.1 ± 24.7
White Oak-Chestnut	4	4587 ± 635	84.5 ± 15.1
Red Oak-Pignut Hickory	2	651	6
		4373	105.5
Red Spruce	2	0	0
		2590	46.1
Eastern Hemlock	2	0	0
		2511	36.3
Chestnut Oak-Chestnut	1	1129	20.4

studies these two forest types were given primary consideration. A site on Rich Mountain near Highlands, North Carolina, was chosen because it is representative of oak forests along the Blue Ridge Mountains, it is the location of a mature chestnut oak-chestnut forest and the mountain is symmetrical thus giving a composite of all directional slopes. The study area on Rich Mountain ranges in elevation from 975 m to 1101 m at the top, encompasses approximately 35 ha and is the site of a chestnut oak-chestnut forest. A total of eighteen 20 × 20 m^2 quadrats was measured in this forest tract along 8 compass directions similar to those given for Steestachee Bald in Figure 2. A second site for a detailed study was selected on Steestachee Bald along the Blue Ridge Parkway near Waynesville, North Carolina. A red oak-chestnut forest occurs on the south-facing slope and a gray beech forest covers the north-facing slope above the Parkway. Maps of the locations of the 30 survey sampling sites and the topography and location of the sampling sites on Steestachee Bald are presented in Figures 1 and 2, respectively.

Nitrogen fixation rates were measured during the early summer of 1978 using the acetylene reduction methods. Portions of the lichen thallus (8 cm^2) were incubated in serum bottles for one hour in 0.1 atm acetylene, following which gaseous samples were trapped (Schell & Alexander, 1970). The trapped gaseous samples were returned to the laboratory for measurement of ethylene production by gas chromatography (Becker et al., 1977). Light intensity and temperature were recorded during the incubation period.

RESULTS

The values for the standard dry wt cm^{-2} of each of the lichen species encountered in this study are presented in Table 1. These values ranged from a low of 8 mg cm^{-2} for the gelatinous foliose lichen *Leptogium cyanescens* to a high of 33.1 mg cm^{-2} for *Parmeliella corallinoides*. A single value is given for *Peltigera polydactyla* and *Peltigera horizontalis,* since these two species are morphologically very similar. Some lichens (in brackets, Table 1) were found infrequently and no dry wt/area estimates could be made, in which case the value of a congener was employed.

Tabulation of the measurements of the survey quadrats confirmed one's personal observations that there was a great deal of variability in the biomass of the lichens present in the various forests (Table 2). Gray beech forests measured along the Blue Ridge Parkway between mileposts 422 and 426 (Fig. 1) supported the most extensive mass of nitrogen fixing lichens (Table 2). However, there was considerable variation in biomass both within and between vegetational types. The reason for the high variability of lichen biomass in the gray beech is due to variation in density of *Aesculus octandra* Marshall (buckeye).

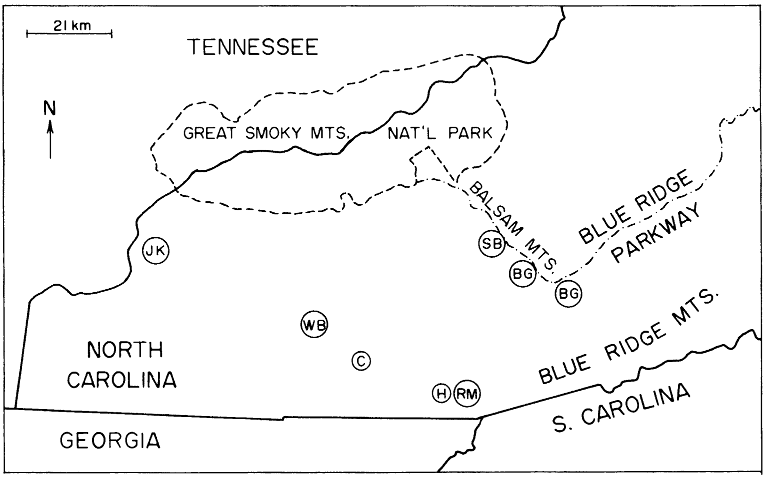

FIGURE 1. Locations of sampling sites for nitrogen fixing lichens. Sampling areas included Joyce Kilmer Memorial Forest (JK), Wayah Bald (WB), Coweeta Hydrological Laboratory (C), Highlands (H), Rich Mountain (RM), Steestachee Bald (SB) and Beech Gap forests (BG).

One quadrat measured in Buckeye Gap at milepost 426 had 19 buckeye trees in it and had a lichen surface area of nearly 120,000 cm^2. This extrapolated to a biomass of approximately 52 kg ha^{-1}. This quadrat was unusual, but lichen biomass values ranging from 7 to 9 kg ha^{-1} were common for these beech gaps. The mean of the gray beech forests of beech gaps was 14.3 kg ha^{-1}.

A compilation of the total surface area represented by the nitrogen fixing lichens in beech gap communities is presented in Table 3. These values resemble those of the tall Douglas fir forest of Oregon (Denison, 1973) in that a *Lobaria* species was the predominant lichen. In Oregon *Lobaria oregana* was the predominant lichen, while in the present study

TABLE 3. Nitrogen fixing lichens from gray beech forests in beech gaps along the Blue Ridge Parkway between mileposts 422 and 430. Data are the totals of five 20 × 20 m^2 quadrats ranging in elevation from 1620 to 1665 m.

Lichen Species	Lichen Surface Area (cm^2)	Percent of Total Lichen Surface Area	Biomass (g ha^{-1})
Lobaria quercizans	84,435	51.0	8359
L. pulmonaria	57,018	34.5	4932
Collema subflaccidum	14,808	8.9	763
Leptogium cyanescens	4173	2.5	167
Sticta weigelii	2461	1.5	234
Pseudocyphellaria crocata	1411	0.9	135
Leptogium chloromelum	618	0.4	25
Nephroma helveticum	178	0.1	10
Peltigera canina	168	0.1	10
Parmeliella corallinoides	102	0.1	17
Peltigera polydactyla	70		4
Leptogium corticola	20		1

TABLE 4. Summary of vegational analysis of the chestnut oak-chestnut forest on Rich Mountain and abundance of lichens found on bark substrate. Importance value is the sum of relative density, relative dominance and relative frequency.

Tree and Shrub Species	Importance Value	Lichens (cm^2 ha^{-1})	Lichen Selectivity Coefficient
Quercus prinus L.	0.518	6399	12.4
Kalmia latifolia L.	0.277		
Acer rubrum L.	0.264	1961	7.4
Cornus florida L.	0.257	1470	19.9
Rhododendron maximum L.	0.233		
Quercus velutina Lam.	0.181	2944	16.3
Pinus strobus L.	0.167		
Oxydendrum arboreum (L.) DC.	0.151	1077	7.1
Quercus rubra L.	0.102	1026	10.1
Carya tomentosa (Poiret) Nuttall	0.088	3398	38.6
Pinus rigida Miller	0.071		
Quercus alba L.	0.071	1177	16.6
Nyssa sylvatica Marshall	0.068	1013	15.0
Robinia pseudo-acacia L.	0.063		
Hamamilis virginiana L.	0.062	7	0.1
Castanea dentata (Marshall) Borkh.	0.056		
Carya glabra (Miller) Sweet	0.046	97	2.1
Liriodendron tulipifera L.	0.044		
Halesia carolina L.	0.043	93	2.2
Clethra acuminata Michaux	0.033		
Cornus amomum	0.030		
Sassafras albidum (Nuttall) Nees.	0.029	305	10.5
Rhododendron calendulaceum (Michaux) Torrey	0.027		
Carya ovalis (Wang.) Sargent	0.022	212	9.6
Others	0.082		

L. quercizans and *L. pulmonaria* were most abundant, contributing about 85% of the total lichen surface area. The gelatinous foliose lichens *Collema subflaccidum* and *Leptogium cyanescens* were also very common and together constituted >11% of the nitrogen fixing lichen surface area. Of the total lichen surface area in the gray beech forest approximately 94% was found on the bark of buckeyes.

Lobaria quercizans and *L. pulmonaria* were common in oak forests. However, here another lichen *Sticta weigelii* commonly equaled or exceeded the abundance of the *Lobaria* species. The lichen biomass in the oak forest was generally much lower than that in the gray beech forest (Table 2) except for occasional sites on mountain ridges and tops. Cove forests proved to be poor locations for these lichens and none were found on conifers. The few N-fixing lichens living in red spruce and hemlock forests (Table 2) grow on the few deciduous trees in these forests and not on the conifers.

The results of the survey quadrats (Table 2) prompted more detailed investigations on the abundance and diversity of these nitrogen fixing lichens. Two sites were chosen, a chestnut oak-chestnut forest on Rich Mountain at Highlands and a forest on Steestachee Bald near Waynesville. A vegetation analysis of the forest on Rich Mountain was completed and is summarized in Table 4 together with data on lichen abundance. Total lichen surface area was calculated; and in order to attain some measure of which tree species serve as favorable substrates for these lichens, the lichen abundance (cm^2 ha^{-1}) was divided by the importance value of the tree or shrub species and multiplied by 10^{-3}. This value

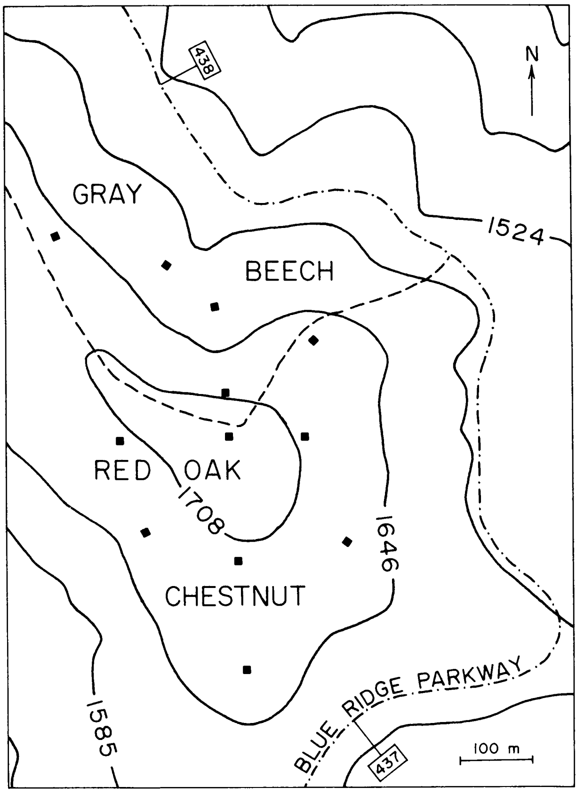

FIGURE 2. Topographic map of Steestachee Bald prepared from a U.S. Geological Survey map of the Waynesville quadrangle. Location of sampling quadrats in the gray beech and red oak-chestnut forests and altitude in meters are indicated. Steestachee Bald is located between mileposts 437 and 438 on the Blue Ridge Parkway.

will subsequently be called the lichen selectivity coefficient and compares the abundance of the lichens to the relative importance of the tree in the forest.

From the data of Table 4 it is apparent that *Carya tomentosa* was the optimum substrate for these nitrogen fixing lichens in this forest community. The oaks, dogwood, black gum and sassafras also served as comparatively good substrates for these lichens. The most abundant lichens were *Sticta weigelii, Parmeliella corallinoides, Leptogium cyanescens* and *Collema subflaccidum* with cm^2 ha^{-1} and percent of total lichen surface areas of 5415 (24.4%), 5045 (23.6%), 3429 (15.2%) and 2390 (11.2%), respectively. Total lichen biomass on Rich Mountain, however, was low at 0.4 kg ha^{-1}.

A similar study was completed for the forest vegetation on Steestache Bald (Fig. 2). The data for the vegetation analysis and measure of the lichens found on the bark substrates are presented in Table 5. Buckeyes were less abundant in this gray beech forest than they were in the beech gaps, nevertheless, they served as excellent bark substrates for the nitrogen fixing lichens. Other favored substrates were *Acer pensylvanicum, Fagus grandifolia* and *Acer saccharum* in the gray beech forest and *Quercus rubra* in the red oak-chestnut forest. The relative abundance and species diversity of the lichens on Stee-

TABLE 5. Summary of vegetational analysis and lichen abundance for gray beech and red oak-chestnut forests on Steestache Bald. Data computations were according to the legends of Tables 1 and 4. A topographical map of Steestachee Bald is given by Figure 2.

Tree and Shrub Species	Importance Value	Lichens (cm^2 ha^{-1})	Lichen Selectivity Coefficient
Gray Beech Forest			
Fagus grandifolia Ehrhart	0.859	43,215	50.3
Betula lutea Michaux f.	0.558	3970	7.1
Acer pensylvanicum L.	0.437	61,625	141.0
Amelanchier arborea (Michaux f.) Fernald	0.237	5790	24.4
Acer spicatum Lam.	0.236	1005	4.3
Ilex ambigua (Michaux) Torrey	0.198		
Aesculus octandra Marshall	0.157	41,310	263.1
Acer saccharum Marshall	0.077	10,200	43.2
Cornus alternifolia L.	0.072		
Rhododendron calendulaceum (Michaux) Torrey	0.034		
Cornus amomum Miller	0.034		
Vaccinium sp.	0.034		
Red Oak-Chestnut Forest			
Quercus rubra L.	1.188	73,884	62.2
Betula lutea Michaux f.	0.338		
Rhododendron calendulaceum (Michaux) Torrey	0.288		
Fagus grandifolia Ehrhart	0.269	1016	3.8
Amelanchier arborea (Michaux f.) Fernald	0.254		
Crataegus sp.	0.181		
Acer rubrum L.	0.112		
Acer spicatum Lam.	0.101		
Others	0.231		

stachee Bald are presented in Table 6. In both the red oak-chestnut and gray beech forests *Lobaria quercizans* was the most abundant nitrogen fixing lichen, as measured both by percentage of lichen surface area and total lichen biomass. However, in the less mesic south facing slope (red oak-chestnut, Table 6), *Sticta weigelii* approached *L. quercizans* in abundance. The gelatinous foliose lichens *Leptogium cyanescens* and *Collema subflaccidum* were present in almost every quadrat, but their contribution to the total lichen biomass was relatively small. *Peltigera* species were not uniformly distributed but generally occurred as large mats over moss on the base of trees.

Nitrogen fixation catalyzed by these lichens also was highly variable, depending upon the moisture condition of the thallus. Fixation only occurred on rainy days and the day following a rain, provided desiccation was not severe. The measurements used in this study were completed on the 8th and 9th of June 1978. The temperature varied from 16–18°C and light intensity from 12–56 μeinsteins m^{-2} sec^{-1}. Mean rates of nitrogen fixation expressed in nmoles per g dry wt per h, the standard error of the mean and the number of replicates were 12,330 ± 2665 (18), 7416 ± 1317 (18), 3997 ± 831 (18), 3876 ± 777 (18) and 36,240 ± 5044 (12) for *Lobaria pulmonaria, Sticta weigelii, Pseudocyphellaria crocata, Parmeliellia corallinoides* and *Lobaria quercizans*,, respectively. The most rapid rate of fixation was catalyzed by the most abundant lichen, *Lobaria quercizans*. Fixation rates could not be correlated with light intensity over this range or with time of day. Meteorological records for Waynesville, Highlands and Franklin revealed that precipitation sufficient to sustain nitrogen fixation could occur for approximately 100 days yr^{-1}.

TABLE 6. Abundance of nitrogen fixing lichens in gray beech and red oak-chestnut forests on Steestachee Bald. Measurements were made and tabulated according to the legends of Tables 1 and 4. A topographical map of Steestachee Bald is given by Figure 2.

Lichen Species	Surface Area (cm^2 ha^{-1})	Percent of Total Lichen Surface Area	Biomass (g ha^{-1})
Gray Beech Forest			
Lobaria quercizans	134,145	80.1	2656
Lobaria pulmonaria	20,845	12.4	361
Leptogium cyanescens	3350	2.0	27
Nephroma helveticum	3125	1.9	36
Sticta weigelii	2445	1.5	48
Collema subflaccidum	1795	1.1	18
Nephroma parile	1430	0.9	16
Peltigera canina	240	0.1	3
Parmeliella corallinoides	160	0.1	5
Red Oak-Chestnut Forest			
Lobaria quercizans	23,303	31.0	461
Sticta weigelii	19,981	26.6	390
Collema subflaccidum	7475	9.9	77
Peltigera horizontalis	5243	7.0	66
Leptogium cyanescens	4121	5.5	33
Nephroma helveticum	4084	5.4	47
Lobaria pulmonaria	2841	3.8	49
Parmeliella corallinoides	2822	3.8	93
Pseudocyphellaria crocata	2331	3.1	45
Peltigera polydactyla	1963	2.6	25
Peltigera canina	828	1.1	10
Pannaria rubiginosa	109	0.1	2
Leptogium corticola	78	0.1	1
Collema conglomeratum	44	0.1	
Leptogium chloromelum	16		
Coccocarpia cronia	13		

Since nitrogen fixation by lichens is light dependent (Kallio et al., 1972; Hitch & Stewart, 1973; Kelly & Becker, 1975), calculations of rates of fixation were based on a 12 h day. From these estimates the mean and standard error of the mean for nitrogen fixation rates for these lichens were calculated to be 54 ± 6 mg N reduced per g dry wt per yr. For each kg dry wt of lichen biomass approximately 54 g of ammonia nitrogen is added to the forest each year in the southern Appalachian Mountains. The mean annual ammonia nitrogen contributions for the gray beech forests in beech gaps (Table 2) and the gray beech and red oak-chestnut forests on Steestachee Bald (Table 6) would, therefore, be approximately 0.77, 0.17 and 0.07 kg ha^{-1} yr^{-1}, respectively.

Discussion

The results of this study indicate that having a propitious bark substrate and having abundant moisture are critical factors affecting the abundance of nitrogen fixing lichens in the southern Appalachian Mountains. The biomass of nitrogen fixing lichens on substrates such as rock or soil was significantly less than that occurring epiphytically in the various forests and is not a factor in the total lichen biomass. Nitrogen fixation, presumably an advantage to these lichens, only occurred when the thallus was wet. The greatest abundance of these lichens consistently was found near the tops of mountains or on high mountainous ridges where exposure to moisture would presumably occur with regularity.

Buckeyes offered the best bark substrates for these lichens. The lichens often grow anywhere from the base of the tree to approximately 8 m or to a point at which the trunk subdivides into the larger branches. Very few small buckeyes are found in the forest, possibly because their fruit is highly prized by rodents, however, for the few small specimens lichen abundance appeared to be correlated with the size of the host tree. In the few instances where buckeyes were found in other forests besides gray beech, lichens were abundant on them but not to the extent found in the beech gap forests. It is not known what feature of buckeye bark makes it a prized substrate for these lichens. Buckeye bark sloughs off in large plates, not the type of substrate which one would associate with long term stability required for the growth of lichens. Perhaps the moisture holding capacity is instrumental in providing this suitability. Since lichens appeared to be so sparsely distributed on conifers, conifer forests were only briefly studied (Table 2). Dey (1978) mentions that *Coccocarpia cronia, Lobaria pulmonaria* and *Sticta fuliginosa* are found in rare instances on *Abies* in the southern Appalachian Mountains. This was not the case in this study; however, a more intensive sampling effort in these forests might have revealed such associations. The presence of conifers does not, however, prevent the establishment and growth of these lichens within the forest, since lichens were often found in abundance on the deciduous trees in the coniferous forest and since branches of *Abies frazeri* (Pursh) Poiret could extend across the trunk of a buckeye with lichens growing profusely upon the trunk of the buckeye. Thus, the southern Appalachia coniferous forests contrast with the tall Douglas fir forest of Oregon where *Lobaria oregana* occurs abundantly in the canopy of a conifer *Pseudotsuga menziesii* (Mirb.) Franco (Denison, 1973; Pike, 1978). From personal observations of many fallen branches and from observations within the canopy, it is clear that the nitrogen fixing lichens locally are only rarely found above 3–4 m on any tree except buckeyes.

One could speculate that desiccation is much more of a problem for these lichens in the southern Appalachian Mountains. Rainfall is abundant there but it occurs more or less continuously throughout the year. In other forests where N-fixing lichens are abundant, such as in tropical rain forests (Forman, 1975), rainfall occurs throughout the year, but in a much greater volume. In the tall Douglas fir forest of Oregon the annual precipitation is similar to that found in the present study area, but it occurs primarily in the winter months (Zobel et al., 1978) and thus keeps the lichens wet and maintains conditions favorable for growth and nitrogen fixation for an extended period of time. This extended moist condition probably does not occur often in the case of the lichens of this study, since they dried out very rapidly following a rain.

Since lichens are slow growing, it could be supposed that the lichen abundance would be greater in a primary forest. Joyce Kilmer Memorial Forest is such a forest and measurements were completed in this forest at elevations ranging from 777–1204 m. Very few lichens were found on large *Lirioderdom tulipifera*. The oak forests within the Kilmer forest also had a smaller lichen biomass than did similar forests either along the Blue Ridge Parkway in the Balsam Mountains or at most sites near Highlands. The level of precipitation in the vicinity of Joyce Kilmer Memorial Forest is 142–152 cm yr^{-1}, less than the 183–200 cm yr^{-1} observed in the areas sampled closer to the Blue Ridge escarpment (Hardy, 1970), perhaps underscoring again the correlation between precipitation and the growth of nitrogen fixing lichens.

The variability in the abundance of the nitrogen fixing lichens in the vegetational types measured (Table 2) reflects to a large extent the differential abundance of favorable tree substrates for their growth. Hickory trees, although good substrates in these mountain forests (Table 4), are not sufficiently common to sustain extensive lichen biomass. Variation in the coniferous forest was largely attributable to the relative availability of hardwood trees as substrates for lichen growth. At locations with high lichen biomass, such as the gray beech forest (Tables 2, 3 & 5), the lichen abundance (primarily *Lobaria*) is determined largely by the presence of buckeyes. The amount of effective substrate also increases in the gray beech forest, partly because lichens are found extending up the trunk of buckeyes. The lichen abundance in red oak-chestnut and white oak-chestnut forests, though substantial, is limited almost exclusively to within 1 m of the ground on suitable trees. These oak forests tend to be less mesic than the sheltered gray beech forests (Whittaker, 1956), and this difference in height of lichen growth may once again be directly correlated with the availability of water.

The Rich Mountain site for the detailed study was selected because it represents a mature oak forest at lower elevations, the mountain is symmetrical and it was convenient to the Highlands Biological Station, the base station for this research. Although the lichen biomass was low (0.4 kg ha^{-1}), a total of 16 different lichen species was found distributed on 14 different species of trees (Table 4). In contrast, the lichen biomass in the red oak-chestnut forest on Steestachee Bald was greater (1.3 kg ha^{-1})—the lichen flora was similar, but these lichens occurred only on two species of trees. The chestnut oak-chestnut forest has many more dominant tree species offering favorable lichen substrates and apparently offers many more types of habitats for lichen growth (Tables 4 & 5).

Ideally one could have selected 2 gray beech forest sites in the beech gaps presented in Table 2; this was not possible. These forest tracts were not large initially, and the construction of the Blue Ridge Parkway divided them to such an extent that they are now relegated to small fragments. In the one instance at Buckeye Gap, where the biomass of lichens is very high and the buckeyes are abundant, the beech gap forest was almost eliminated by the Parkway and an adjacent excavation. Therefore, the tract on Steestachee Bald was measured realizing that it would have a lower lichen biomass.

The characteristics of the lichen floras of the gray beech forest on Steestachee Bald are similar to those of the gray beech forest of beech gaps (Tables 3 & 6). *Lobaria quercizans* is the predominant species with *L. pulmonaria* second and contributing significantly to the lichen biomass. *Acer pensylvanicum* also was commonly employed as a substrate for these lichens, as indicated by the lichen selectivity coefficient 141.0 (Table 5), a value second only to that of the buckeye.

The annual contribution of reduced nitrogen to the forest by these lichens is low, particularly in the oak forests at lower elevations. Based on the estimate of the fixation rate of 54 mg N reduced per g dry weight lichen thallus per year as described in the results section, the annual contribution in the red oak-chestnut forest of Steestachee Bald would be 70 g ha^{-1} yr^{-1}. The value for the gray beech forests would be considerably greater with 770 and 170 g ha^{-1} yr^{-1} for these forests in the beech gaps and Steestachee Bald, respectively. It is realized that these values are estimates but it is still apparent that these lichens are important nitrogen contributors in the gray beech forest. Todd, Waide and Cornaby (1975) have estimated a total annual input of ammonia nitrogen by nitrogen fixation in a mature hardwood forest at Coweeta Hydrological Laboratory near Franklin to be 10.9 kg ha^{-1}. The annual contribution by lichens of 0.8 kg ha^{-1} in the gray beech forest represents a significant portion of this total.

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